IDENTIFICATION OF GEOGRAPHIC FORMS OF COMMON DOLPHIN (*Delphinus delphis*) FROM AERIAL PHOTOGRAMMETRY

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ABSTRACT

At least four morphologically distinct forms of common dolphins are found in the eastern Pacific. We compared length data for common dolphins photographed from the northern, central and southern regions as defined by Perrin *et al.* (1985) and found significant differences in average length for adult animals (>150 cm) and for "adult females" defined for our purposes as animals accompanied by calves. Analyses of calculated birth dates for calves demonstrated differences in timing of reproduction between the geographically adjacent forms. Length distributions from aerial photographs and samples collected from the purse seine fishery were strikingly similar. This work demonstrates a new, noninvasive method for obtaining unbiased life history and morphological data.

Key words: common dolphin, *Delphinus delphis*, geographic forms, length, timing of reproduction, aerial photography, photogrammetry.

Determining the intraspecific structure of the widely distributed and geographically varied common dolphin, *Delphinus delphis*, has been problematic. In fact, over two dozen nominal species have been proposed although currently most authorities recognize one highly varied species (Heyning and Perrin 1991). Evans (1975, 1982) examined the morphology and distribution of this species in the eastern Pacific and described five distinct forms: (1) a short-beaked form off southern California; (2) a short-beaked form off Baja California; (3) a large, long-beaked neritic form north of 20°N; (4) a short-beaked central tropical form; and (5) a southern short-beaked form. He also suggested the possibility of an "equatorial-oceanic" population. Based on more sightings and a larger sample of aged specimens, Perrin *et al.* (1985) combined the southern California and Baja short-beaked populations and expanded the range of the southern form to include Evan's equatorial-oceanic group (Fig. 1). They defined a southern stock based on a hiatus of sightings between the central and southern populations.

Most specimens used in the reports cited above were killed incidental to purse seine fishing for yellowfin tuna (Perrin 1969). The use of fishery samples to obtain data on life history and morphology usually raises questions concerning
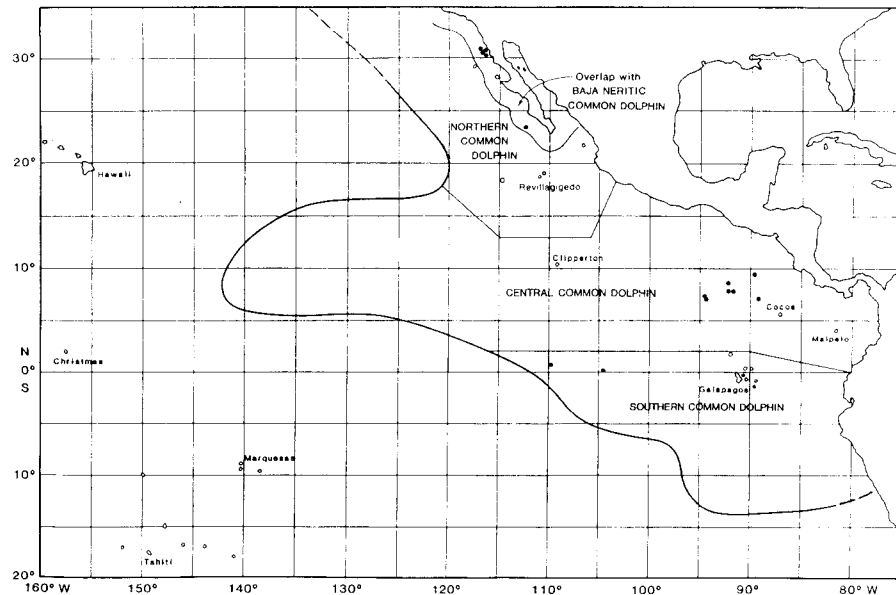
Figure 1. Recommended management units for *Delphinus delphis* from Perrin et al. 1985. Locations of schools used in this report are indicated by dark circles.

potential bias in the sample (*e.g.,* Perrin and Reilly 1984). For example, the vulnerability of dolphins to fishing mortality may vary with age, sex, or reproductive condition. If so, then samples obtained from the fishery are biased, and the validity of studies using these samples are in question. In addition, the geographic distribution of specimens collected from the fishery is restricted to areas where common dolphin and tuna associate.

In this study we avoid the above-mentioned biases by using low-level aerial photogrammetry to examine the geographic forms of free-ranging common dolphins. Length distributions of common dolphins from the northern, central, and southern regions (Fig. 1) were compared. We also compared lengths of adult animals swimming with calves, defined as "adult females," among these regions and examined calculated birth dates of calves for evidence of reproductive seasonality. Similar techniques have been applied to the study of large cetaceans (Scott and Winn 1980; Whitehead and Payne 1976; Cubbage and Calambokidis 1987; Sumich 1984, 1986; Koski *et al.* 1992; Withrow and Angliss 1992), but this is the only large scale application of aerial photogrammetric sampling to the study of geographic concordance of intraspecific differences in small cetaceans (Scott and Perryman 1991).

METHODS

Photographic sampling—Aerial photographs of 14 schools of common dolphins were used for this report (Table 1). We took the photographs from a Hughes 500D helicopter that was deployed from the NOAA Ship *David Starr*

Table 1. Schools of common dolphins used in length comparison study. School size determined by observer estimates or counts from photographs.

Flight date	School position	Estimated school size	Number measured
9/14/88	00°41'N; 109°59'W	155	10
9/17/88	00°02'N; 104°25'W	1,840	40
10/10/88	07°05'N; 089°08'W	870	25
10/16/88	08°49'N; 092°08'W	649	57
12/1/88	23°25'N; 112°19'W	343	72
10/19/89	07°56'N; 091°55'W	226	68
10/19/89	07°54'N; 092°02'W	167	57
11/15/89	07°04'N; 094°16'W	30	9
11/15/89	07°03'N; 094°16'W	377	37
10/15/90	09°35'N; 089°36'W	125	85
12/5/90	30°10'N; 116°16'W	562	171
12/5/90	30°16'N; 116°12'W	1,175	393
12/5/90	30°31'N; 116°15'W	600	43
12/5/90	30°47'N; 116°22'W	1,100	274

Jordan. This sampling was part of a research program conducted by the National Marine Fisheries Service to monitor trends in size of dolphin stocks that are killed incidental to purse seine fishing for yellowfin tuna (Holt and Sexton 1989).

The photographs were taken with a KA45A military reconnaissance camera that was mounted vertically below the fuselage of the helicopter. The camera was designed to collect high resolution, medium format (127 mm) images from high-speed aircraft flying at low altitudes. It has a medium focal length, fixed focus lens (152 mm), with a maximum aperture of f2.8. The camera's focal plane shutter consists of two metal curtains that sweep a slit of light along the film plane, parallel to the direction of flight. When used from a moving platform, this type of shutter can cause some distortion and blurring of the image due to the relative movement between the camera and the scene. The KA45A counteracts this problem with a forward image motion compensation (FMC) system that moves the film at precisely the same speed and direction as the image while the shutter is open. The speed of film movement is a function of altitude and ground speed. FMC reduces distortion and greatly improves image resolution.

All of the photographs were taken with Kodak Aerial Plus-X black and white film. We exposed the film through a medium yellow filter (Wratten #9) to reduce the amount of blue light reaching the film, thus enhancing the contrast between the dolphins and their blue background. The photographs were taken at altitudes between 200 and 300 meters and at a ground speed of about 113 km/hr. As each frame was exposed, a computer-based data acquisition system automatically logged both the altitude and time. This system also allowed the scientists in the helicopter to record other information for each pass over the school.

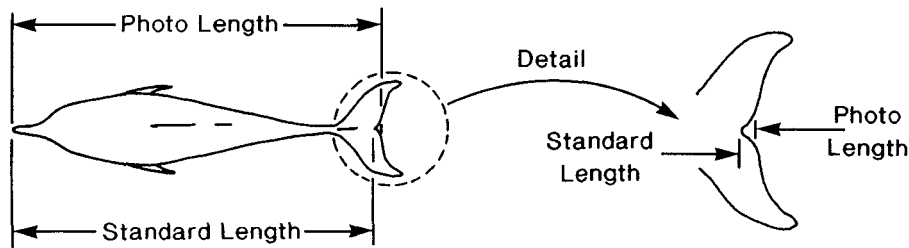*Length determination*—We selected dolphins for measurement that were

Figure 2.   Illustration of the difference between standard length and length measured from aerial photographs.

swimming parallel to and very near the surface. Dolphins that were jumping, surfacing, or diving were excluded from the sample. We measured the dolphins from the tip of the rostrum to the trailing edge of the tail flukes (Fig. 2). We selected these points because the fluke notch was very difficult to see in most of the images. For adult specimens this measurement is about 2.5 cm longer than standard length (Norris 1961).

We measured the dolphins on the original negatives with the aid of a stereocomparator, which records distance measurements to the nearest micron. A micron corresponds to roughly 1.5 mm on the ground from our normal sampling altitude of 230 m. These measurements were supplemented and verified with a variable ocular micrometer installed in a stereo zoom microscope.

In vertical photographs the relationship between the size of an object and its image on the film is determined by the ratio of the focal length of the lens and the distance from the camera to the object. This ratio is commonly called the scale of the photograph and is defined as scale $= A/f = o/i$ where $A =$ altitude, $f =$ lens focal length, $o =$ size of object photographed, and $i =$ size of the image of the photographed object.

In our study focal length remained constant and the scale of each image was determined by the altitude recorded from the radar altimeter. To calibrate the radar altimeter, we photographed objects of known size (target arrays ashore and the ship at sea) and compared altitude derived from measurements with recorded altitude.

Measurement precision and accuracy—There are several potential sources of error in determining the true size of an object from its image on an aerial photograph. In topographical aerial photogrammetry, objects of known size and configuration can be photographed and then measured to determine accuracy of a photographic sampling system. When aerial photogrammetry is applied to the study of marine mammals, known-sized animals are generally unavailable and indirect techniques must be used to estimate the magnitude of the errors inherent in the sampling. In this study we conducted three experiments to examine the accuracy and precision of our data.

To test the effect of varying altitude of photography on the accuracy of our measurements, we photographed three painted dolphin targets from altitudes of 200, 240, and 260 meters, the range of altitudes we used in the field. We painted the dolphins light blue-grey against a darker blue background to

simulate the low subject to background contrast we encountered over the tropical Pacific. Measurements of known-sized objects near the targets were used to determine the scale of each image. For each pass the three dolphins were independently measured ten times in sequence by two individuals.

Because measuring targets was probably easier than measuring dolphins swimming under water, we also tested the precision of our length measurements by repeatedly measuring five dolphins from a single photograph. We selected dolphin images of varying quality and of both adults and calves. The test was performed rapidly and at the end of eight hours of measurement in an attempt to add the element of fatigue to the sample.

In addition to errors in measurement of the images, errors in instantaneous readings of altitude, image distortion from tip or tilt of the camera, and the refraction of light as it passes through the water all impact the accuracy of our dolphin length measurements. Also, the flex of the bodies of the dolphins associated with normal swimming movements changes their apparent length when viewed from above. Dolphins that were moderately arched or tilted were easily eliminated from the data set because their rostrums or flukes were not visible from above. However, measurements of animals that were slightly arched or tilted still remain in the data set and our estimates of the true length of these dolphins are likely negatively biased.

To determine the variability in the measurements associated with all these sources of error, we examined the data for dolphins that were measured in three or four photographs from the same pass. In this exercise and the two described above, we used the coefficient of variation as a measure of the relative precision of the measurements. We also compared a subset of our length sample with published data taken from specimens to determine whether the biases associated with the different sampling regimes produced different results.

Data analysis—Our photographs included schools from each of the three management units recommended by Perrin *et al.* (1985; Fig. 1). In the northern region, a short-beaked and a much larger long-beaked form occur sympatrically but apparently do not school together (Evans 1975). We examined the length distributions of the schools from this region first to determine the stock mix in this sample. Only data for the short-beaked form were used in comparisons among the three regions.

In Perrin *et al.* (1985) morphological differences between putative stocks of common dolphins were demonstrated by comparing the means of length distributions for mature male and female specimens from the northern and central regions. Obviously, we could not directly examine the sexual characters of the dolphins in our photographs, so we devised two methods for stratifying our length samples for comparison with the strata used by Perrin and his co-workers. These two methods and a technique for detecting reproductive seasonality are described below.

Method #1—modes—Our length distributions from each region included a small sample of calves and young animals and a larger sample mode containing subadult and adult age classes (Fig. 3). We eliminated the youngest animals from the samples using length as the limiting criteria (<150 cm) and tested
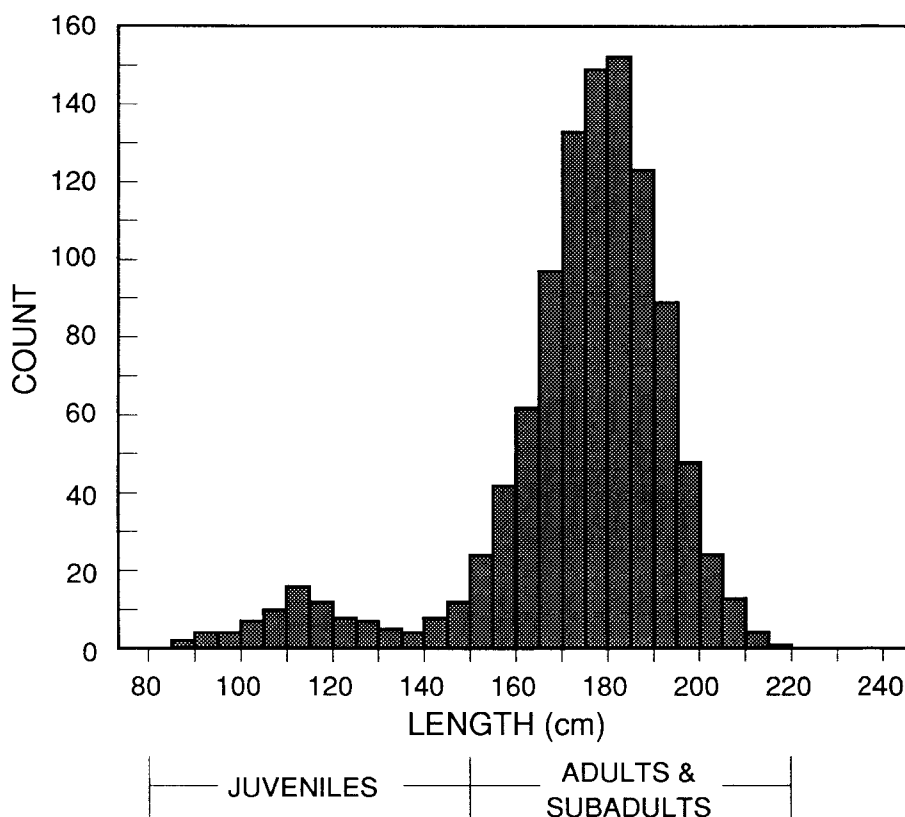
Figure 3.   Histogram of lengths for common dolphins from the northern region.

for regional differences in size with an ANOVA. We selected the Tukey-Kramer procedure for pair-wise comparison because of its power in tests with unequal sample sizes (Day and Quinn 1989). Because the selection of 150 cm as a minimum size for this sample was somewhat arbitrary, we repeated the analysis with minimum values of 155, 160 and 165 cm.

Method #2—"adult females"—The unique association between cows and calves has been noted for a wide range of cetaceans (Norris and Prescott 1961, Taber and Thomas 1982, Wells and Scott 1990, Pryor and Shallenberger 1991), and this behavior has been used to identify cows or adult females in several studies (Whitehead and Payne 1976, Würsig and Würsig 1980, Sumich 1984, Cubbage and Calambokidis 1987, Best 1990, Jones 1990, Scott and Perryman 1991, Miller *et al.* 1992, Koski *et al.* 1993). In our aerial photographs, calves (dolphins <145 cm) were consistently found swimming closely alongside a larger animal (>155 cm). The distance between these cow-calf pairs was about one-fourth that between dolphins of approximately adult size. Based on the consistency of this association in all of our images and the work cited above, we have assumed that the larger animal swimming closely alongside a calf was

an adult female. Because this determination was made entirely on behavior, we qualify the term with quotation marks, "adult females," whenever we are referring to a sample of lengths based on the above assumption. We conducted an additional ANOVA as described above to test the hypothesis that "adult females" from the three regions did not differ in length.

Reproductive seasonality—Typically, postnatal growth in delphinids is very rapid and almost linear for the first year. During this period when increases in length are large relative to the variability in length at age, seasonal modes in length distributions and frequency histograms of back-projected birth dates have been used to investigate patterns of growth and reproductive seasonality for several stocks of tropical dolphins (Perrin *et al*. 1976, Perrin *et al*. 1977, Barlow 1984, Perrin and Henderson 1984, Hohn and Hammond 1985).

For common dolphins a very limited amount of information is available on growth rates from specimens taken in the eastern Pacific (Hui 1973). In our first analysis of reproductive seasonality, we used estimates of average length at birth for the northern (81.3 cm) and central (79.0 cm) stocks and assumed that length at birth for the southern stock was the same as in the north. We used the estimated length at 1 yr of 135 cm that Hui (1973) reported for common dolphins taken off southern California and Baja California, Mexico as our best estimate of the average length at 1 yr for all three stocks. Assuming linear growth during the first year, we back-projected the birth dates for all dolphins < 135 cm in length.

We generated a second distribution of back-projected birth dates using the published lengths at birth (80 cm) and one year (123 cm) for the northern spotted dolphin (Hohn and Hammond 1985). We selected the spotted dolphin as the model for this second data set because of its similarity in size to the common dolphin and the large body of published information on growth for this stock of tropical dolphins.

We used Kuiper's modification of Kolmogorov's test (modified K test) for comparisons of circular distributions (Batschelet 1965) to test the hypothesis that these birth-date distributions were uniform (as done by Barlow 1984). This is a nonparametric test for goodness-of-fit for cumulative distributions. Because critical values for two-tailed tests have not been tabulated, this test was only applied in comparisons of sample distributions with uniform distributions.

All statistical tests not specifically referenced were performed with the program Super ANOVA distributed by Abacus Concepts, Inc., Berkeley, California. Tests were considered significant at $P < 0.05$ unless stated otherwise.

RESULTS

Altitude calibration—We compared calculated altitude (A_m) from measurements of known-sized objects with simultaneous readings from our radar altimeter and found a consistent bias in the recorded altitudes (A_r). The linear regression equation shown below describes the relationship between A_m and A_r.

$$A_m = 1.013A_r - 33.755 \qquad (r^2 = 0.993) \tag{1}$$

Table 2. Lengths for three painted dolphin targets measured independently by two individuals (A and B). Each length is the mean of 10 measurements. True target length is in parentheses.

Altitude (m)	Dolphin target no. 1 (84.6 cm)		Dolphin target no. 2 (177.4 cm)		Dolphin target no. 3 (191.5 cm)	
	A	B	A	B	A	B
200	84.9	84.4	175.7	174.3	190.7	191.3
240	85.1	86.1	176.6	178.7	191.1	192.1
260	86.3	85.7	176.3	178.0	192.8	192.8

For each school, this formula was used to correct the recorded altitude before the lengths of the dolphins were calculated.

During the 1990 field season the radar altimeter failed and was returned to the manufacturer for repairs. When the instrument was reinstalled, we recalibrated it and found that the relationship between A_m and A_r had changed. The new relationship was

$$A_m = 1.016A_r - 12.211 \qquad (r^2 = 0.992) \qquad (2)$$

This relationship was used to correct the recorded altitude during the last two legs of the 1990 survey.

Accuracy and precision in length determination—For half of the 18 samples the measurements of the dolphin targets from the aerial photographs were within 1 cm of the true length of the painted dolphin figures (Table 2). The measurements from the lowest altitude were consistently smaller for all targets and interpreters, but the differences between lengths for this range of altitudes were too small to require corrections or a modification in sampling techniques.

Repeated measurements of targets or animals from a single photograph indicate that the errors associated with the measurement process are very small (Table 3). When we compared measurements for the same dolphin in three or four different frames, the mean and range for the coefficients of variation increased but still remained at an acceptably low level. The additional variability in different

Table 3. Measurement precision, expressed as coefficients of variation, for replicate measurements of dolphin-shaped targets and of dolphins from single frames, and for measurements of dolphins from 3–4 successive frames.

Measured object	No. dolphins measured	Measurements per dolphin	Mean of CVs	Range of CVs
Dolphin targets individual A	3	30	0.008	0.005–0.012
Dolphin targets individual B	3	30	0.014	0.007–0.020
Dolphins in one frame	5	5	0.009	0.004–0.012
Dolphins in different frames	54	3–4	0.026	0.001–0.083

Table 4. Comparison of published length information for adult female common dolphins (Perrin *et al.* 1985, Heyning and Perrin 1991) with lengths of "adult females."

Data source	Neritic or long-beaked	Northern	Central	Southern
Specimen data				
n	10	82	306	6
Mean	207.7	178.5	194.3	188.5
SD	—ᵃ	7.30	6.80	6.86
Range	193–224	155–200	170–215	180–198
Photographic data				
n	5	100	41	20
Mean	206.2	179.2	194.8	184.3
SD	13.40	8.79	8.96	6.80
Range	185–217	159–200	169–212	172–197

ᵃ Not reported.

frames probably resulted from scale errors (imprecision in altimetry, camera tip or tilt, and refraction), which can introduce either a negative or positive bias, and the change in apparent length associated with swimming movements, which should result in a negative bias.

Finally, we compared the means of our length samples of "adult females" from the northern and central regions with comparable published data for adult females (Table 4) and found no significant differences (*t*-test; $P > 0.40$). We chose not to test for differences between our sample and published data for the neritic or southern stocks because of the small amount of data available for comparison.

Length distribution comparisons—Four of the five schools from the northern region were found in the shallow, nearshore habitat occupied by both the short-beaked and the larger ($\sim$28 cm for adult females; Heyning and Perrin 1991) neritic or long-beaked forms of common dolphin (Table 5). When we compared the average lengths of dolphins $>$150 cm and of "adult females" for the five schools from this area, it was obvious that the animals in one of the schools

Table 5. Depth, distance to shore, and size data for common dolphin schools photographed off of Baja California.

School no.	Distance to shore (km)	Depth (m)	Mean length (>150 cm)	Mean length (cm) "adult females"
1	19	164	205.6	206.2
2	27	182	180.6	182.3
3	19	155	181.3	179.1
4	16	150	177.8	180.3
5	103	3,300	168.8	172.8

Table 6. Summary of mean lengths and results of Tukey-Kramer pairwise tests for the northern (Nor), central (Cen) and southern (So) regions.

	Mean length comparisons		
Subsample criteria	Nor/Cen (cm)	Cen/So (cm)	Nor/So (cm)
>150 cm	179.0/191.9**	191.9/183.8**	179.0/183.8*
>155 cm	179.6/192.4**	192.4/183.8**	179.6/183.8*
>160 cm	180.7/193.1**	193.1/184.8**	180.7/184.8*
>165 cm	182.0/193.3**	193.3/185.7**	182.0/185.7
"Adult females"	179.2/194.8**	194.8/184.3**	179.2/184.3*

$* P < 0.05; ** P < 0.01.$

were much larger on average (about 25 cm) than those from any of the other schools. Based on this size difference and the agreement of our data on this school with published lengths for specimens from the long-beaked form of common dolphins, we identified the animals in this school as long-beaked common dolphins and did not use these lengths in any of the regional comparisons that follow.

We conducted an ANOVA to test the hypothesis that the length samples (Fig. 4) for dolphins >150 cm from the three regions did not differ and the hypothesis was rejected ($P < 0.01$). The Tukey-Kramer *post hoc* tests found that all three regions differed significantly from one another when the minimum lengths for the samples were 150, 155, and 160 cm (Table 6). At 165 cm, the northern and southern regions no longer differed significantly, but they both differed from the central region at the $P < 0.01$ level.

When we repeated the analysis using only data for "adult females" (Fig. 5) from each region, we found significant differences ($P < 0.01$) between the central sample and the northern and southern samples. The northern and southern samples differed at the 0.05 level.

Birth-date distributions—Our analysis of the distribution of the back-projected birth dates revealed three distinct patterns of reproductive seasonality (Fig. 6). In the northern region most births occurred in the first six months of the year although some calving occurred throughout the year. This pattern was found to differ significantly ($P < 0.01$) when compared (modified K-test) with a projected uniform distribution (Fig. 7). In the central region, the back-projected birth dates were distributed throughout the year, and the modified K-test revealed no significant difference between the sample and a uniform pattern of births ($P > 0.10$). The sample from the southern region showed the strongest seasonality, with all calving occurring during the first six months of the year. This distribution differed significantly from the uniform ($P < 0.01$). When we repeated these analyses using birth-date distributions generated from the published average size at birth and at one year for spotted dolphins (Hohn and Hammond 1985) to determine the rate of growth, the peaks in reproduction shifted in timing but the relative patterns and test results remained the same (Fig. 8).
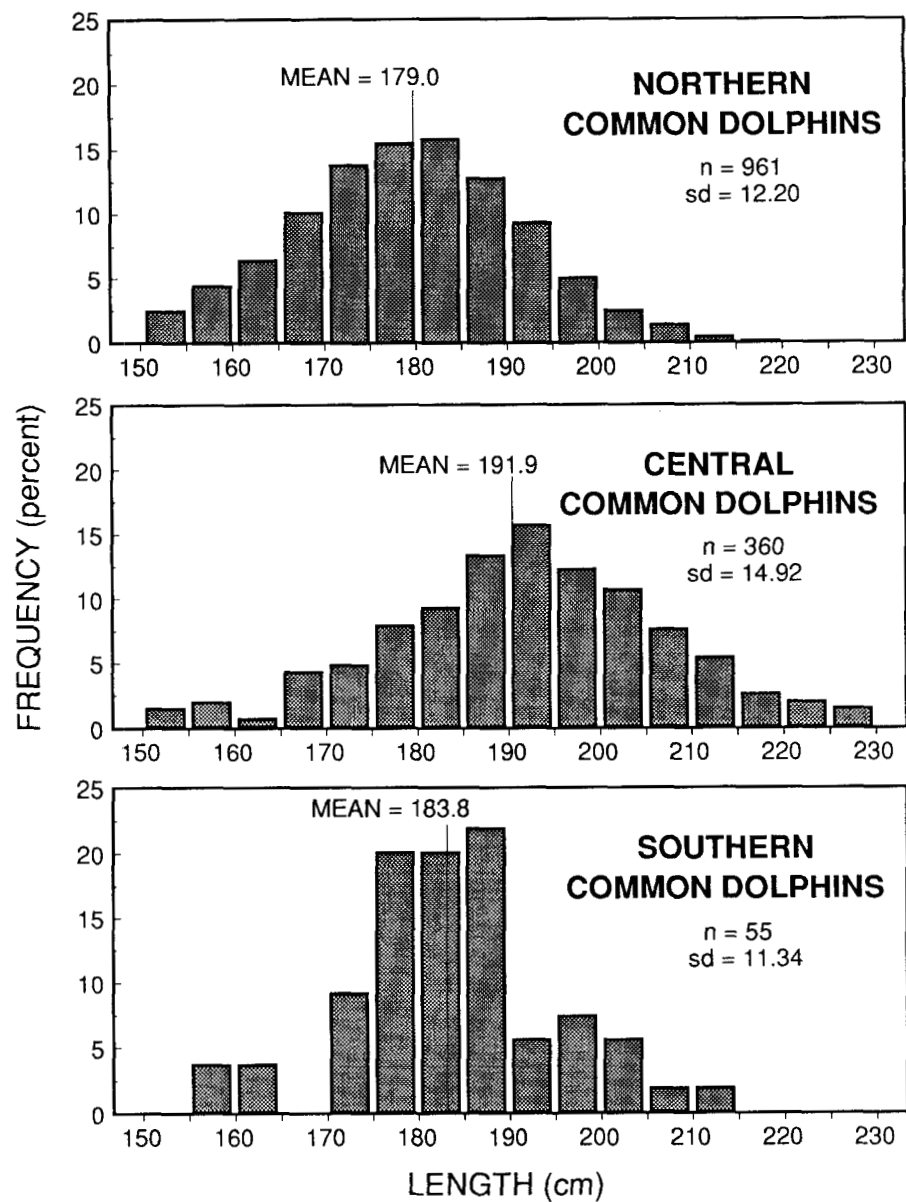
Figure 4.   Length-frequency distributions and means for common dolphins ≥ 150 cm from the northern, central and southern regions. Sample size and standard deviation included for each data set.
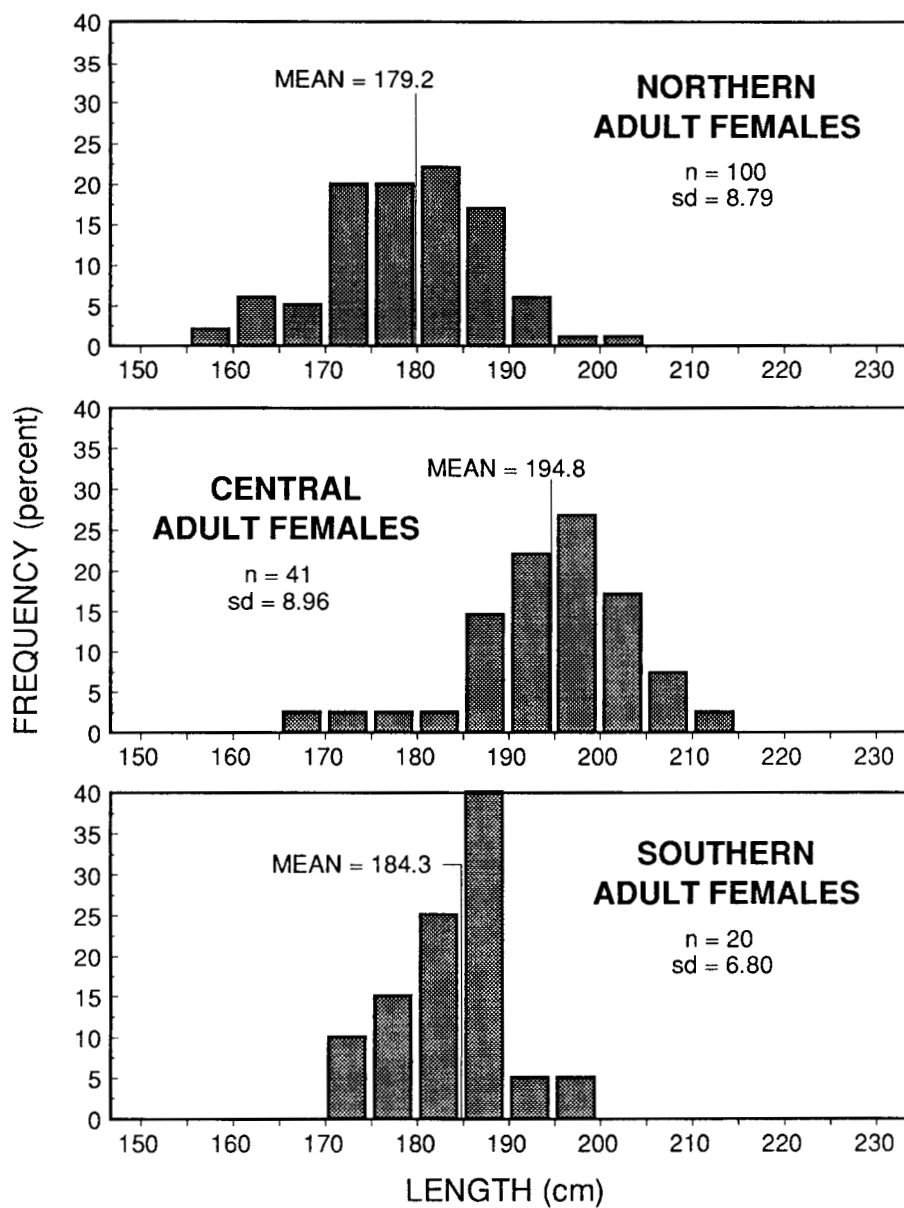
Figure 5. Length-frequency distributions and means for "adult females" from the northern, central, and southern regions. Sample size and standard deviation included for each data set.
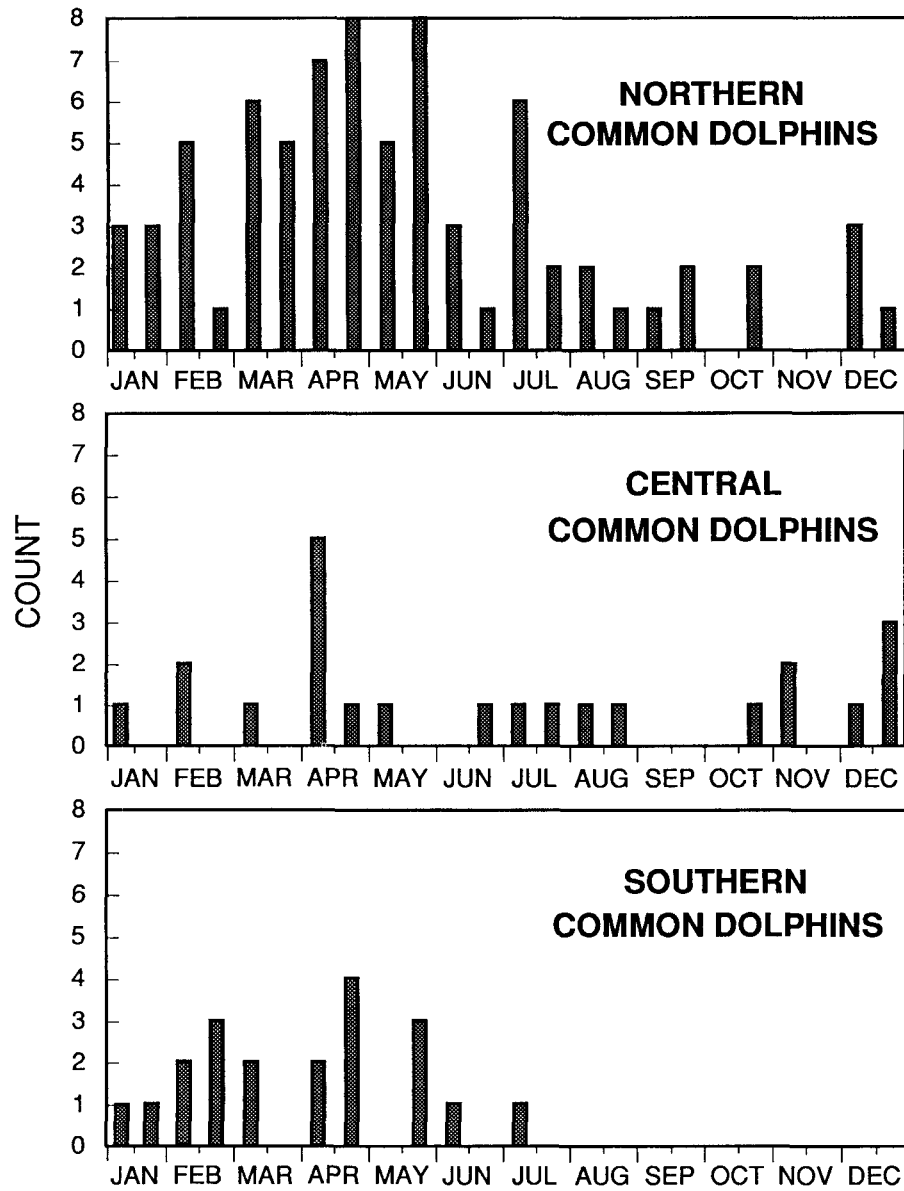
Figure 6.   Distribution of calculated birth dates for common dolphins from three geographic areas.

DISCUSSION

The accuracy of the target measurements (average error <1%) and the precision of repeated measures from a single image (CVs average ≈0.01) reported here are very similar to those documented in several other aerial photogrammetric
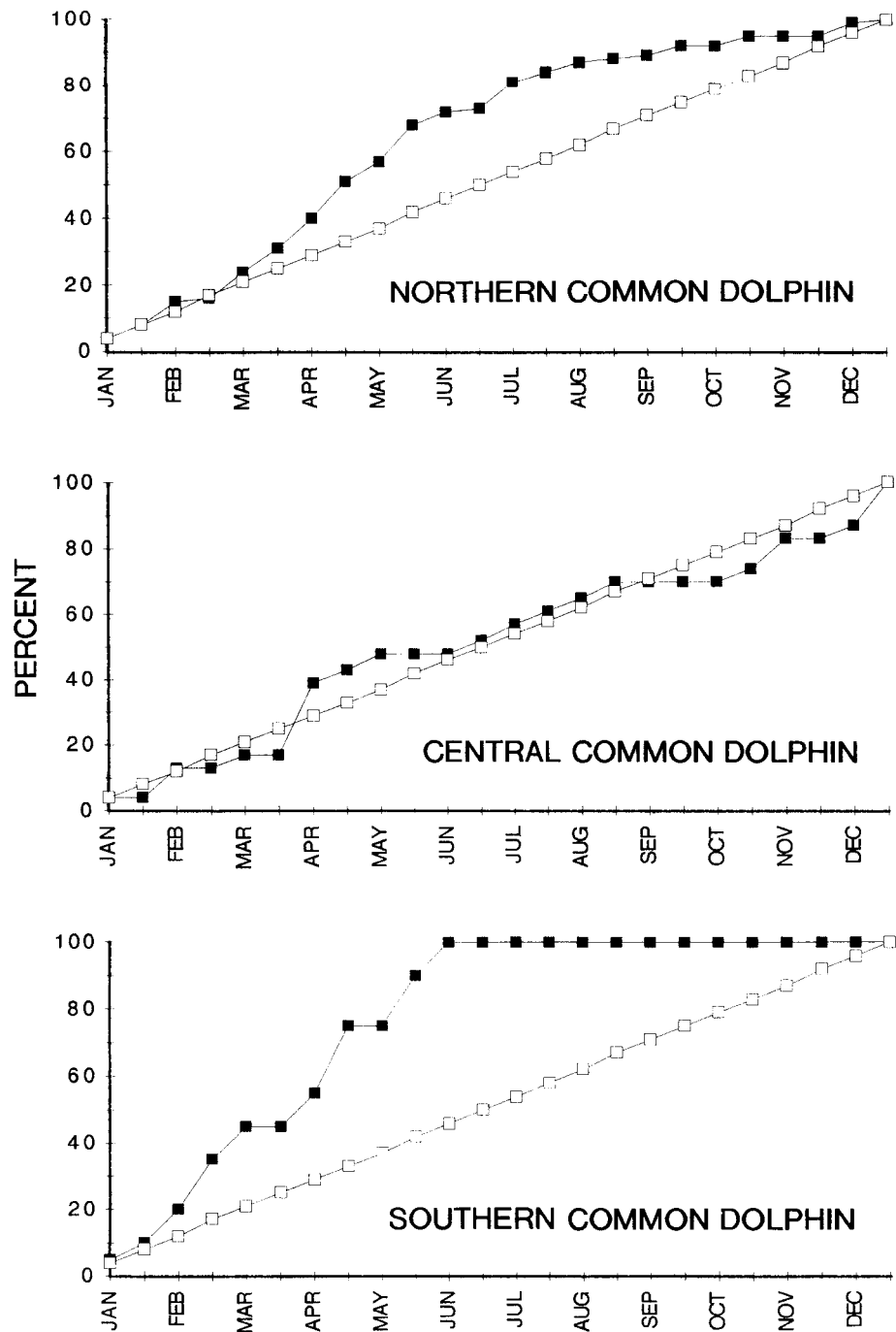
Figure 7.   Cumulative distribution of calculated birth dates for common dolphins from the northern, central, and southern regions. Plot of open boxes represents cumulative distribution of births if births were uniform throughout the year; closed boxes represent estimated cumulative distribution of births.
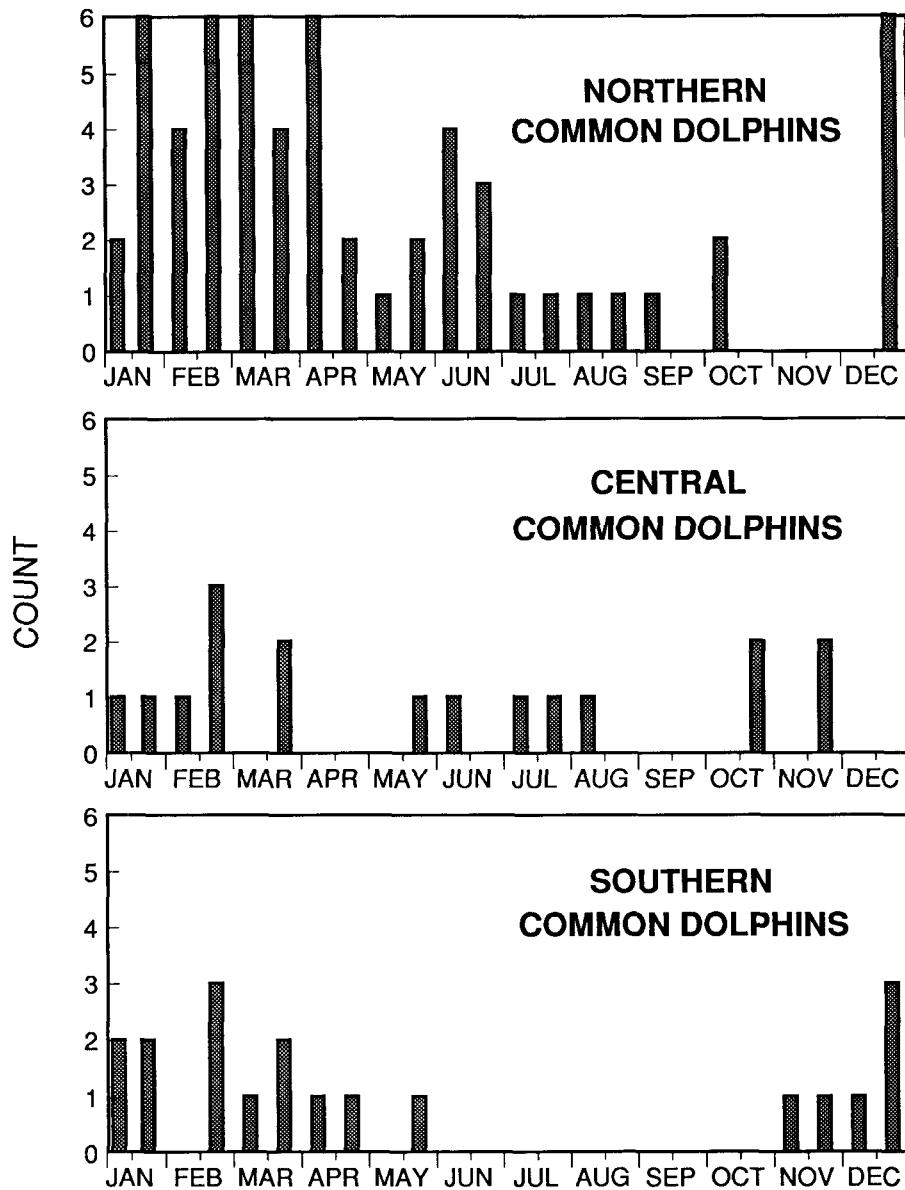
Figure 8. Distribution of calculated birth dates for common dolphins from three geographic areas using published data for the northern spotted dolphin to generate growth rates.

field studies (Croze 1972, Scott and Winn 1980, Cubbage and Calambokidis 1987, Koski *et al.* 1992). We also compared the lengths of dolphins measured from three or more successive frames to estimate the amount of variability in length determination resulting from errors in altitude measurement and the flex

of the dolphins. As we expected, these measurements were more variable and the average of the coefficients of variation increased to 0.026. These data are comparable with average CVs of 0.014 and 0.024 for repeated photographs of gray and bowhead whales (Sumich 1984, Koski *et al.* 1992).

There are two known sources of bias in the length data that we presented in this paper. We measured to the trailing edge of the fluke rather than to the base of the fluke notch, which introduced a positive bias of about 2.5 cm for adult dolphins. Also, for an unknown proportion of the dolphins that we measured, the flex of their bodies and their orientation relative to the water's surface caused us to underestimate their length. These extremely small biases appear to have counterbalanced each other because there were no significant differences between the means of our length samples and those from previous studies that used specimens (Table 4).

We calculated the birth dates of dolphins approximately ≤ 1 yr old to see if there was any evidence for differences in reproductive seasonality, which could provide a barrier to gene flow between adjacent putative stocks. By this effort we are not trying to imply that we can accurately determine the age of a young dolphin from a length measurement. Rather, we think that by applying the same technique to geographically isolated groups of dolphins we can detect differences in patterns of reproduction.

In the more temperate environments to the north and south, we found a pulse in reproduction from January through July. Reproductive seasonality was strongest in the southern stock which inhabits the region that displays the widest range of oceanographic parameters of the three (Au and Perryman 1985, Fieder 1992). In the more typically tropical surface waters, which provide the habitat for the central stock, reproduction was distributed evenly throughout the year. This pattern of strong reproductive seasonality in the southern habitat in contrast to the more even distribution of births in the tropical waters to the north is similar to that demonstrated for spotted dolphins (Barlow 1984).

The data that we have reported here support the recommendations by Perrin *et al.* (1985) that common dolphins sighted within 185 km of the Pacific coast of Baja must be identified to stock based on size, beak length, and color pattern rather than by location. Based on differences in length between the northern and central putative stocks, and a hiatus in distribution between the southern and central stocks, the same authors recommended that the northern, central, and southern populations of short-beaked common dolphins should be managed as separate units. We have strengthened that argument by demonstrating differences in morphology between the southern and central regions and detecting differences in reproductive seasonality between adjacent regions. However, our data for the southern stock were drawn from only two schools that were found at the eastern edge of the distribution for this geographic form. More sampling of the southern form is needed to determine whether these data are representative of the entire southern region.

The results of the initial application of our length sampling system are very encouraging. We have developed a technique for collecting information on morphology and life history of small pelagic cetaceans that is independent of

fishery-induced mortalities. This provides us with a tool for examining potential biases in our existing life history data base and the ability to sample in areas or seasons in which the fishery is not active.

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